

A REVISION OF THE CLASPING-LEAVED *POTAMOGETON* (POTAMOGETONACEAE)

ROBERT R. HAYNES

*Aquatic Biology Program, Department of Biology
P.O. Box 1927, University of Alabama
University, AL 35486, U.S.A.*

The genus *Potamogeton* Linnæus has long been considered to be one of the more taxonomically difficult and more ecologically important genera of all the aquatic vascular plants. These difficulties and importances have been summarized earlier (Haynes 1974, 1978) and will not here be discussed. Because of the importance and taxonomic confusion, I have begun a taxonomic revision of the genus.

Potamogeton is a cosmopolitan genus with approximately 100 species of submersed and floating-leaved aquatic plants. The genus has been separated into two subgenera (Raunkiaer 1896) and numerous sections and subsections (Ascherson and Graebner 1907; Hagström 1916). My approach has been to prepare treatments of one or a few subsections at a time, without considering whether the subsection should be recognized, and eventually to combine all these treatments into one volume for the entire genus. At that time the infrageneric classification will be re-evaluated and a treatment presented. This paper concentrates on two quite small subsections, subsection *Perfoliati* Graebner and subsection *Praelongi* Hagström.

Representatives of these two subsections are the only species of the genus with clasping leaves, these leaves all submersed. As a result, Ascherson and Graebner (1907) combined them in subsection *Perfoliati*, although Raunkiaer (1903) had earlier separated them into two groups, these groups without formal rank. Hagström (1916) followed Raunkiaer in separating the groups, naming the *P. praelongus*-group of Raunkiaer subsection *Praelongi*. Fernald (1932) and Ogden (1943) accepted Hagström's taxonomy without comment.

The morphological features, as well as the flavonoid chemistry, are evidence for combining the two subsections into one. However, the stem anatomy is quite different between representatives of the two subsections. Although my inclinations are to combine the two subsections, I do not understand the within and between subsectional variability of the above mentioned characteristics, as well as the other characteristics.

The nomenclature and morphology of the genus, including descriptions, have been published earlier (Haynes 1974, 1978) and will not be restated here.

The treatment that follows is based on extensive field study, growth of plants in similar and varied conditions, cytological examination, chemical examination, and an examination of over 3000 herbarium specimens from the following 26 herbaria: AAU, ALU, B, BM, BR, C, CAN, DA0, F, G, GH, LE, K, M, MEL, MO, NSW, NY, P, S, TI, UNA, US, V, W, Z, (abbreviations according to Holmgren et al. 1981). Keys are based upon materials containing fruits; dimensions of leaves are taken from the fully expanded, longest leaves of a specimen; measurements of widths are taken approximately at the widest point of the leaf; and descriptions of fruits are taken strictly from mature structures.

KEY TO THE SUBSECTIONS OF CLASPING-LEAVED *POTAMOGETON*

1. Leaf apex cucullate; fruits with dorsal keel, 4–5.7 mm long *Praelongi*
1. Leaf apex non-cucullate (flattened); fruits without dorsal keels, 1.6–4.2 mm long *Perfoliati*

POTAMOGETON subsection *PRAELONGI* Hagström, Kongl. Svenska Vetenskapsakad. Handl. 55(5):250. 1916. TYPE: *Potamogeton praelongus* Wulfen. Characteristics of the species.

1. *POTAMOGETON PRAELONGUS* Wulfen in Roemer, Arch. 3:331. 1805. TYPE: AUSTRIA. Labuch, 8 Jun 1763, *Wulfen s.n.* (ISOTYPE: MEL!).

P. flexuosum Wredow, Mecklenb. Fl. 1807.

P. flexicaulis Dethard, in Sterlitzer Anzeig., no. 50. 1809.

P. perfoliatus L. var. *lacustris* Wallman in S. Liljebl., Utkast Sv. Fl. 706. 1816.

P. acuminatum Wahlenb., Fl. Upsal. 116. 1820.

P. salicifolius Wolfg. ex Fries, Summa Veg. Scand. 1:213. 1845.

Spirillus praelongus (Wulfen) Nieuwland, Amer. Midl. Naturalist 3:17. 1913.

Stems very pale green, simple or branched near apex, terete without nodal glands, to 210 cm long, to 3 mm diam. Leaves usually pale green, rarely olive-green, delicate, mostly alternate, rarely opposite, 11–33-nerved, 8–28 cm long, 1.1–4.6 cm wide; apex cucullate; lacunae absent; stipules white, fibrous, convolute, free from leaf blade, shredding at apex, persistent, 3–8.1 cm long, 3–8 mm wide. Winter buds (turions) absent. Peduncles cylindrical, terminal or axillary, erect to spreading, 9.5–53 cm long, 1–4 mm diam. Spikes cylindrical, 3.4–7.5 cm long, 1–2 cm diam; verticels 7–10, separated by 3–8 mm. Perianth segments 2–3.5 mm long, 1.5–2.5 mm wide; anthers 1.1–2.5 mm long. Fruit olive-green, with dorsal keel, occasionally with lateral keels, widest at or above

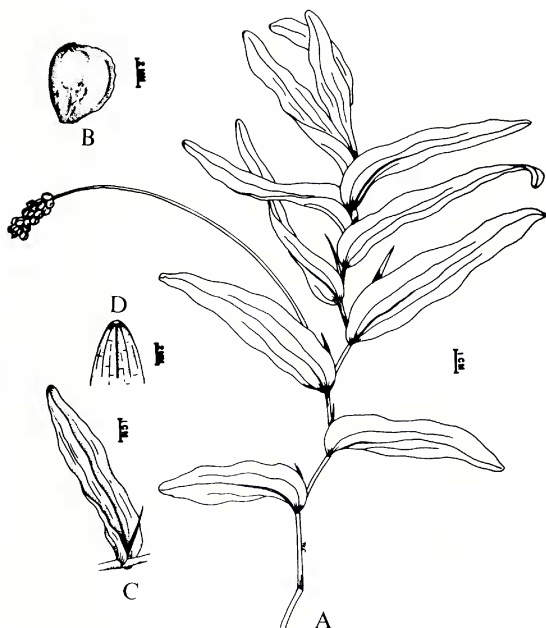


Fig. 1. *Potamogeton praelongus*. A. Habit sketch with axillary inflorescence. B. Fruit. C. Enlargement of node with stipule. D. Enlargement of leaf apex with cucullate tip.

middle, 4–5.7 mm long, 3.2–4 mm wide; beak erect, marginal, 0.6–1 mm long, 0.6–0.9 mm diam; sides rounded or occasionally with slight central bulge; wall texture mostly wrinkled, rarely smooth. Chromosome number, $2n = 52$.

STEM ANATOMY: The stem anatomy of *Potamogeton praelongus* is characterized by a central stele with seven to nine separate vascular bundles. Ogden (1943) considered this type of stele to be the most primitive and thus labelled it "prototype." The endodermis is composed of U-cells. These

are cells that are thickened on the inner and lateral faces and thin on the outer face. The stem also has interlacunae bundles (vascular bundles at the junctures of walls separating the lacunae), subepidermal bundles (vascular bundles directly underneath the epidermis), and a pseudo-hypodermis of several layers of cells immediately beneath and adjacent to the epidermis.

FLAVONOID CHEMISTRY: The leaf flavonoid chemistry of *Potamogeton praelongus* is the most diverse of any species of the genus reported to date. Roberts and Haynes (submitted) isolated nine flavonoid compounds from the species. These include luteolin aglycone and its glycosides, 7-O-glucoside and 7-O-glucuronide, isoorientin, apigenin aglycone, and its glycosides, 7-O-monoglucoside and 7-O-diglucoside, and chrysoeriol aglycone and its 7-O-glucoside.

DISTRIBUTION: Apparently circumpolar in the Northern Hemisphere. In the Western Hemisphere, from north-central Alaska to southeastern Labrador, south to southern Newfoundland, Maryland, southeastern Colorado, and the Aleutian Islands; also central Mexico and the east-central coast of Greenland. The species, in the Western Hemisphere, reaches its northern limit about latitude 73°N and southern limit about latitude 38°N, disregarding the one Mexican locality. In the Eastern Hemisphere, from northwestern Norway to western Russia, south to west Yugoslavia, west to east-central France and northern Ireland; also Kamchatka Peninsula, southwest to east-central Japan. In the Eastern Hemisphere, the species reaches its northern limit about latitude 68°N and southern limit about latitude 35°N.

Although I have seen no material from the vast majority of Russia, the species undoubtedly occurs there. Juzepczuk (1934) lists the species from all parts of the country.

Potamogeton praelongus, with its zig-zagging stem, semi-clasping leaves, and cucullate leaf tips, is one of the most easily recognizable species of pondweeds. The species has been known to hybridize with *P. perfoliatus* on occasion and to produce a sterile off-spring which can perpetuate itself by vegetative methods. The most commonly collected locality for the hybrid is Varming Lake on the Ribe River near Ribe, Denmark. That lake has now been altered considerably and probably does not exist anymore. With the destruction of the lake, the hybrid apparently was extirpated.

POTAMOGETON subsection PERFOLIATI Graebner in Ascherson and Graebner, *Pflanzenr.* 4(11):92. 1907. Type: *Potamogeton perfoliatus* L.

Plants submersed in fresh or brackish waters, perennial. Stems branched or unbranched, terete, without nodal glands. Leaves all submersed, pellucid, sessile, without lacunae, lanceolate to orbicular, obtuse to acute at

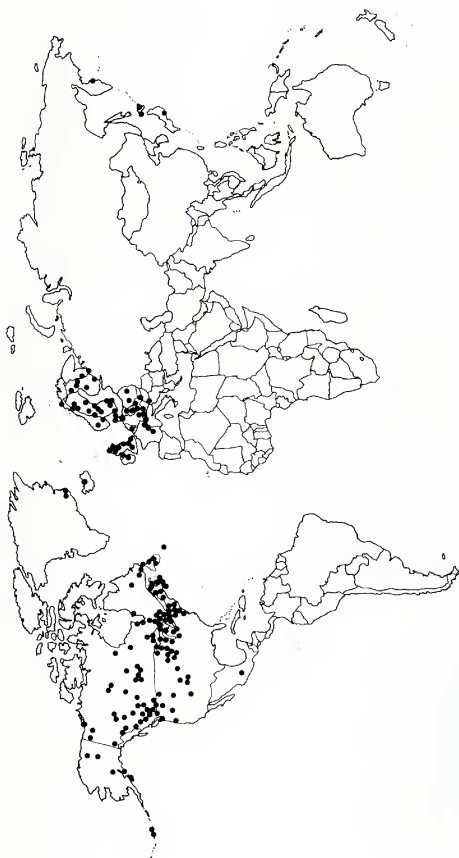


Fig. 2. *Potamogeton praelongus*. Documented distribution.

apex, clasping at base, entire, 3–35-nerved. Stipulates convolute, free from base of blade. Winter buds (turions) absent. Inflorescence emersed, a cylindrical spike with 3–11 whorls of flowers, compact, mostly with 4 flowers at each whorl. Fruit dorsally rounded or keeled, to 4.2 mm long. Chromosome number, $2n = 52$.

KEY TO THE SPECIES

1. Stipules fibrous, persisting as fibers; leaf apex mostly acute; fruits 2.2–4.2 mm long *P. richardsonii*
1. Stipules delicate, without fibers, mostly decaying early; leaf apex mostly obtuse, rarely acute; fruit 1.6–3 mm long *P. perfoliatus*

2. POTAMOGETON PERFOLIATUS L., Sp. Pl. 1:126. 1753. TYPE: SWEDEN/FINLAND. Lappland. *Linnaeus* (LECTOTYPE here designated: Institute de France, Paris, B. Delessert Library; photo of lectotype, BM!).

Potamogeton amplexicaulis Kar. Bull. Soc. Nat. Mosc. 173. 1839.

P. bupleuroides Fernald in Gray, Manual ed. 7. 75. 1908.

P. loeselii Roem. & Schultes, Syst. Veg. 3:508. 1818.

P. perfoliatus L. var. *bupleuroides* (Fernald) Farwell, Amer. Midl. Naturalist 8:264. 1923.

P. perfoliatus L. var. *caudiformis* Aschers. & Graebn., Syn. Mitteleur. Fl. 1:314. 1897.

P. perfoliatus L. var. *cordatilanceolatus* K. Merr. & W. Koch. in Rohl., Deutschland. Fl. ed. 3. 1:852. 1823.

P. perfoliatus L. var. *densifolius* G. Mey., Chloris Han. 523. 1836.

P. perfoliatus L. var. *gracilis* Fr., Novit. Fl. Suec. Alt. 42. 1828.

P. perfoliatus L. var. *loeselii* (Roem. & Schultes) Aschers. & Graebn., Syn. Mitteleur. Fl. 1:314. 1836.

P. perfoliatus L. var. *mandschuriensis* A. Benn., Annuaire Conserv. Jard. Bot. Genève 9:100. 1905.

P. perfoliatus L. var. *prolixus* Hagström, Kngl. Svenska Vetensk. Acad. Handl. 55(5):254. 1916.

P. perfoliatus L. var. *pseudodensus* Aschers. & Graebn., Syn. Mitteleur. Fl. 1:314. 1897.

P. perfoliatus L. var. *rotundifolius* Sonder, Fl. Hamb. 98. 1851.

Spirillus perfoliatus (L.) Nicuwl., Amer. Midl. Naturalist 3:17. 1913.

Stem pale green, simple or branched near apex, terete, to 2.5 m long, 0.2–1.9 mm diam. Leaves usually olive-green, delicate, 3–25-nerved, 0.9–7.6(–9.7) cm long, 0.7–4 cm wide; apex mostly round, rarely acute; lateral nerves joining midrib at apex. Stipules translucent, delicate, not shredding at apex, convolute, fugacious, 3.5–6.5 cm long, 1–1.5 mm diam. Peduncles cylindrical, terminal or axillary, erect to rarely recurved, 1–7.3 cm long, 0.5–2.2 mm diam. Spike cylindrical, 0.4–4.8 cm long, 4.5–8 mm diam; verticels 3–9, separated by 1.5–3 mm. Perianth segments 1.3–2.1 mm long, 0.7–1.9 mm wide. Anthers 1–1.2 mm long, 0.2–0.7 mm wide. Fruit light green to brown, without dorsal keel, widest at or above middle, 1.6–3 mm long, 1.3–2.2

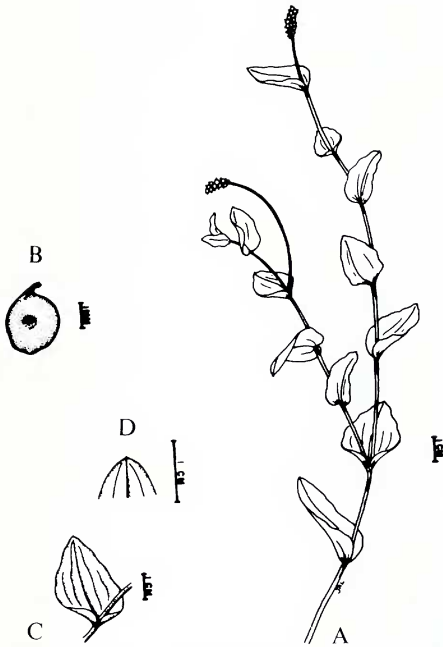


Fig. 3. *Potamogeton perfoliatus*. A. Habit sketch with axillary and terminal inflorescences. B. Fruit. C. Enlargement of node after stipule has decayed. D. Enlargement of leaf apex with flattened (non-cucullate) tip.

mm wide; sides mostly depressed, occasionally rounded; beak central, 0.1–0.9 mm long, 0.1–0.9 mm diam.; wall texture smooth. Chromosome number, $2n=52$.

STEM ANATOMY: The stem anatomy of *Potamogeton perfoliatus* is characterized by a "trio-type" stele (see discussion of *P. richardsonni* for explanation). The endodermis is composed of O-cells, cells that are thickened on

all—inner, lateral, and outer—faces, giving an appearance of an O. The stems also possess a pseudo-hypodermis, but lack interlacunae bundles and subepidermal bundles (see discussion under *P. praelongus* for an explanation of these tissues).

FLAVONOID CHEMISTRY: The leaf flavonoid chemistry of *Potamogeton perfoliatus* is more complex than *P. richardsonii*. Roberts and Haynes (submitted) isolated seven compounds from the species. These include luteolin aglycone and its glycosides, 7-O-glucoside and 7-O-glucuronide, apigenin aglycone and its 7-O-monoglucoside, and chrysoeriol aglycone and its 7-O-glucoside. Harbourne and Williams (1976) isolated a C-glycoflavone from the species. Roberts and Haynes (submitted) did isolate the C-glycoflavone, isoorientin, from the related species *P. praelongus* and this very possibly is the C-glycoflavone which Harbourne and Williams isolated from *P. perfoliatus*.

DISTRIBUTION: In the Western Hemisphere, from Labrador to Newfoundland and SW to southern Ontario and North Carolina; also Lake Atitlán, Guatemala, east-central coast of Greenland, northeastern Iceland, and the Gulf of Mexico outer coastal plain from western Florida to eastern Louisiana. In the Eastern Hemisphere, widespread from extreme northern Norway to western Kamchatka Peninsula, Russia, south to southern Japan, southern India, and northern Spain; also, southeastern Australia, eastern Sudan, and southeastern Algeria.

Potamogeton perfoliatus, morphologically, is extremely variable, especially in Europe. As a result, the taxon has been divided into two specific and 10 or more subspecific categories. These segregates were based exclusively on vegetative variability. After examining hundreds of specimens, I have been unable to divide the morphology into ranges which warrant taxonomic recognition. This variability is continuous, with no geographical distinctions. I have, therefore, decided not to accept any subspecific categories.

Potamogeton perfoliatus var. *muelleri* Bennett was published based upon several collections by Mr. Mueller from southeastern Australia. I have visited the type locality and have examined the type specimen, as well as several others taken from the type locality. In my opinion, the taxon is not *P. perfoliatus* and I am, therefore, excluding it from further consideration at this time.

3. POTAMOGETON RICHARDSONII (A. Benn.) Rydberg, Bull. Torrey Bot. Club 32:599. 1905. TYPE: U.S.A. Michigan, *Robbins s.n.* (LECTOTYPE: GH!).
P. perfoliatus L. var. *lanceolatus* J. W. Robbins in A. Gray, Man. ed. 5. 488. 1867, *non* Blytt 1861.
P. perfoliatus L. var. *richardsonii* A. Benn., J. Bot. 27:25. 1889.

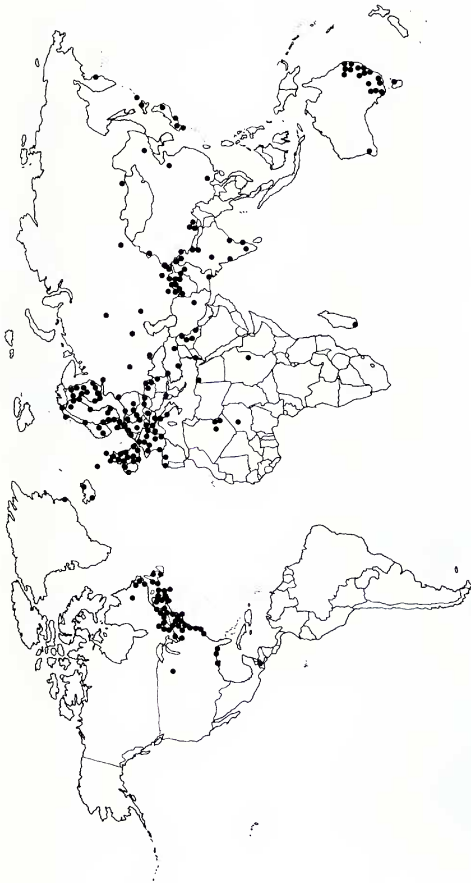


Fig. 4. *Potamogeton perfoliatus*. Documented distribution.

P. perfoliatus L. ssp. *richardsonii* Hultén, Fl. Alaska & Yukon 102. 1940.

Spiralis perfoliatus (L.) Nieuwl. var. *richardsonii* (A. Benn.) Nieuwl. Amer. Midl. Naturalist 3:17. 1913.

Stem pale green, simple or occasionally branched near apex, terete, ca 97 cm long, 1–2.8 mm diam. Leaves lanceolate, usually olive-green, delicate, 3–35-nerved, 1.6–13 cm long, 0.5–2.8 cm wide; apex acute to obtuse; lateral nerves joined midrib at apex. Stipules white, fibrous, shredding at apex, mostly persistent as fibers, 1.2–1.7 mm long, 1–3.2 mm diam. Peduncles clavate, terminal or axillary, erect to rarely recurved, 1.5–14.8 cm long, 1–3.9 mm diam. Spike cylindrical, 1.3–3.7 cm long, 5–11 mm diam.; verticels 5–11, separated by 2–5 mm. Perianth segments 1.1–2.5 mm long, 1–2.4 mm wide. Anthers 1.5–1.6 mm long, 0.5–0.6 mm wide. Fruit light green to brown, mostly without dorsal keel, widest at or above middle, 2.2–4.2 mm long, 1.7–2.9 mm wide; beak central, 0.1–1.1 mm long, 0.1–0.9 mm diam; sides rounded, rarely centrally depressed; wall texture smooth. Chromosome number, $2n = 52$.

STEM ANATOMY: The stem anatomy of *Potamogeton richardsonii* is characterized by a central stele in which three of the four median bundles have united to form a "trio" bundle. There are, therefore, only two bundles in the median region of the stele, one of them with two patches of phloem on the inner face. Ogden (1943) designated this stele as the "trio-type" and considered it an advancement over the proto-type but still not the most advanced type. The endodermis is composed of O-cells. These are cells that are thickened on all-inner, lateral, and outer—faces, giving an appearance of an O. The stems also possess a pseudo-hypodermis, but lack interlacunae bundles and subepidermal bundles (see discussion under *P. praelongus* for an explanation of these tissues).

FLAVONOID CHEMISTRY: The leaf flavonoid chemistry of *Potamogeton richardsonii* is less diverse than *P. perfoliatus*. Roberts and Haynes (submitted) isolated five compounds from the species. These include luteolin aglycone, and its glucosides, 7-O-glucoside and 7-O-glucuronide, and chrysoeriol aglycone and its 7-O-glucoside. Harbourne and Williams (1976) isolated a C-glycoflavone from the species. Roberts and Haynes (submitted) did isolate the C-glycoflavone, isoorientin, from the related species *P. praelongus*, and this very possibly is the C-glycoflavone which Harbourne and Williams isolated from *P. richardsonii*.

DISTRIBUTION: From Aleutian Islands, central Alaska, and Mackenzie Delta to central Quebec, south to New York, Ohio, Colorado, and northern California.

Potamogeton richardsonii has been included with *P. perfoliatus* (Ascherson

and Graebner 1907) and accepted at the specific level by Ogden (1943) and Hagström (1916). The two taxa are quite easily separated over the vast majority of their ranges. In areas of sympatry, however, the two taxa are difficult to separate. This apparent integradation is evidence for recogni-

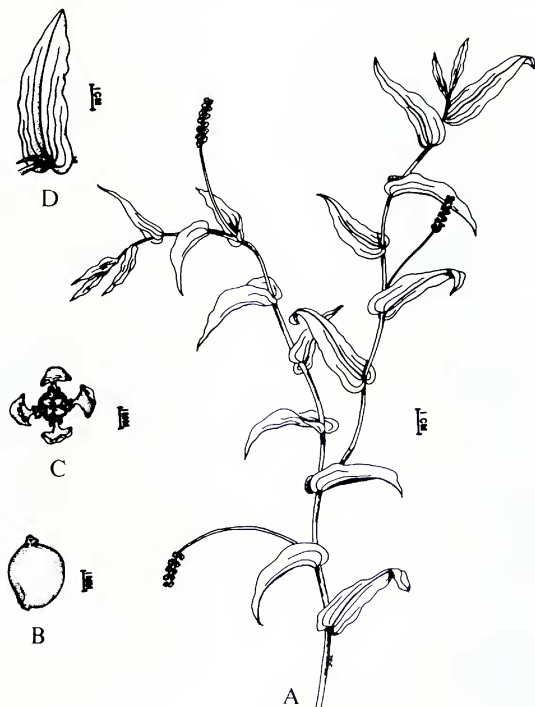


Fig. 5. *Potamogeton richardsonii*. A. Habit sketch with axillary inflorescences. B. Fruit. C. Flower. D. Enlargement of node with persistent stipule.

tion at a subspecific level. These intermediate forms, however, are almost always sterile. If flowers develop, these flowers rarely produce fruit. Should some subspecific category be warranted, one would expect the intermediates produced in an area of sympatry to be fertile, at least fairly commonly.

To test the hypothesis that the two taxa are distinct and should be accepted at the specific rank, individuals of the two taxa were grown in similar conditions (both flowing and non-flowing) in the aquatic biology facility at the University of Alabama. The individuals of the two taxa remained morphologically distinct over the duration of the growth period.

Also, 77 specimens of the complex were examined for 16 morphological characteristics (see Table I). These specimens were taken at random from a group of specimens, each of which possessed all the characteristics measured, including both mature flowers and mature fruits. These specimens were tentatively identified to species, 32 as *P. perfoliatus* and 45 as *P. richardsonii*. The data were analyzed by the NT/SYS statistical package (Rolf, et al. 1977). The specimens were sorted into two groups by the statistical program, the 32 originally determined as *P. perfoliatus* in one group and the 45 originally determined as *P. richardsonii* in the other group.

TABLE I

CHARACTER	P. PERFOLIATUS (N = 32)			P. RICHARDSONII (N = 45)		
	RANGE	X	S.E.	RANGE	X	S.E.
Stem diameter (mm)*	0.2-1.9	0.92	0.78-1.05	1.0-2.8	1.73	1.58-1.88
Leaf width (cm)	0.7-2.6	1.2	1.05-1.35	0.7-2.8	1.24	1.1-1.37
Leaf length (cm)*	0.9-3.8	1.9	1.6-2.2	2.2-10.2	4.4	3.9-4.9
Number vcins	3-21	9.9	8.1-11.7	3-35	12.5	10.1-14.9
Peduncle length (cm)*	1.0-7.3	3.6	3.2-4.0	1.5-11.6	5.4	4.5-6.3
Peduncle diameter (mm)*	0.5-2.2	1.4	1.1-1.7	1.0-3.9	2.2	2.0-2.4
Spike length (cm)*	0.4-4.8	1.4	1.0-1.8	1.3-3.7	2.5	2.3-2.7
Spike diameter (mm)*	4.5-8.0	6.4	5.9-6.9	5.0-11.0	8.0	7.2-8.8
Number inflorescence verticels*	3-9	5.0	4.4-5.6	5-11	8	7.5-8.5
Perianth length (mm)	1.3-2.1	1.52	1.41-1.63	1.1-2.5	1.71	1.61-1.81
Perianth width (mm)	0.7-1.9	1.27	1.17-1.37	1.0-2.4	1.61	1.36-1.86
Fruit length (mm)*	1.6-2.8	2.26	2.15-2.37	2.2-4.2	2.9	2.79-3.01
Fruit width (mm)*	1.3-2.2	1.8	1.7-1.9	1.7-2.9	2.3	2.2-2.4
Fruit beak length (mm)	0.1-0.9	0.45	0.39-0.51	0.1-0.9	0.55	0.50-0.60
Fruit beak width (mm)*	0.1-0.9	0.32	0.27-0.37	0.1-0.9	0.44	0.40-0.48
Number fruits per spike*	3-35	10.8	7.6-14.0	1-65	21.3	16.54-26.1

X—Mean for all measurements of that characteristic.

S.E.—Range of two standard errors above and two standard errors below the mean of that characteristic.

*—Indicates characteristics for which there is no overlap of the two species of the two standard errors above and two standard errors below the mean.

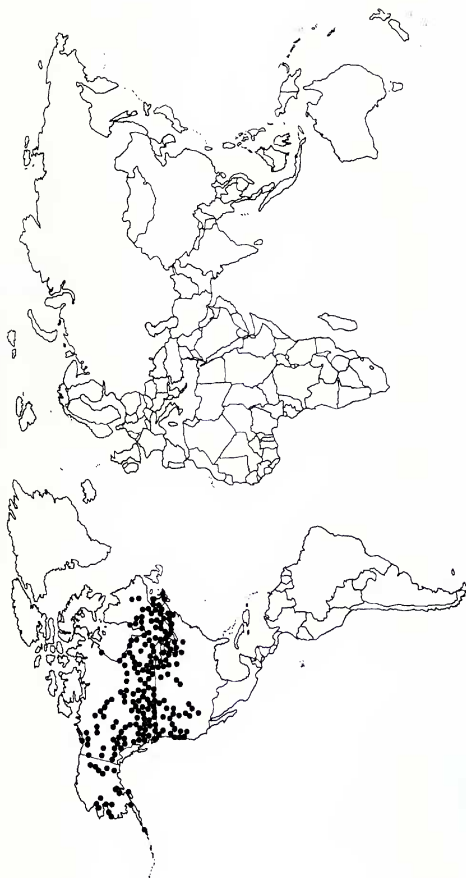


Fig. 6. *Potamogeton richardsonii*. Documented distribution.

The means and standard error were calculated for each group for each characteristic. Table I lists the range for each characteristic, the mean for that characteristic, and the range of two standard errors above and two standard errors below the mean. Whenever there is no overlap between the standard error ranges of a particular characteristic for the two taxa, then that characteristic is considered to be statistically valid in separating the two taxa. The standard error ranges do not overlap for 11 of the characteristics examined. These characteristics are indicated with an asterisk in Table I.

The growth studies and the statistical analysis, along with the phytoecography of the species in North America, lead me to the conclusion that the taxa should be accepted at the species level.

The chemical data can be used to help understand the origin of *Potamogeton richardsonii*. Hagström (1916) proposed that *P. richardsonii* evolved by hybridization of *P. praelongus* and *P. perfoliatus*. Ogden (1943) did not accept that theory since either one of the putative parents is or both are absent over much of the range of *P. richardsonii*. Neither luteolin aglycone and its two glycosides nor chrysoeriol aglycone and its glycoside may be used as evidence for or against the hybrid origin theory. However, apigenin and its monoglucoside are quite helpful as both these compounds are shared by the two putative parents, although in trace amounts in *P. perfoliatus*. Neither compound has been detected in *P. richardsonii*, although large quantities of plants have been extracted. The chemical profile of hybrid taxa is normally additive of the two putative parents (Haynes and Williams 1975), although novel compounds may be found in the hybrid (Ordnuff et al. 1973). The chemical data, with apigenin aglycone and its monoglucoside being present in both putative parental species and being absent in the putative hybrid, support Ogden's (1943) theory that *P. richardsonii* arose by means other than hybridization of *P. praelongus* and *P. perfoliatus*.

Hultén (1937) proposed that there were two main refugia in North America—the Rocky Mountains and the continental shelf outside eastern North America—where plants survived during continental glaciation. From these refugia, he stated, the plants probably spread in an easterly and westerly direction, respectively, toward the center of the continent. Some taxa probably survived in one area, while other taxa possibly survived in both areas. Some of the taxa which survived in both refugia migrated until their ranges overlapped; thus, they now have a continuous range across North America. For others, however, migration ceased before the ranges overlapped. Hultén conceded that species surviving in other areas south of the glacial boundary did migrate north and, to some extent, into the once

glaciated lands. However, he suggested that a much smaller proportion of the species now found in the glaciated areas survived in the vast areas south of maximum glaciation than in the two other refugia.

I propose that *Potamogeton perfoliatus* was, prior to the glacial period, a circumpolar species, with a more or less continuous distribution, including North America. Glaciation would have separated this North American population into two smaller allopatric ones, one to the east and one to the west. During glaciation, the two populations differentiated, resulting in each population evolving into a different species. Once the period of glaciation was complete and the distributions overlapped, the reproductive barriers that had been established during glaciation evidently now prevent gene flow from one population to the other. The western population represents *P. richardsonii* and the eastern *P. perfoliatus*. Iltis (1965) indicated that *Gentianopsis procera* and *G. crinita* possibly had a similar history. Apparently species or varieties could have evolved in a matter of 10,000 years. One need only examine a few of the Great Lakes endemics, e.g. *Iris lacustria* (Guire and Voss 1963), *Cirsium pitcheri* (Johnson and Iltis 1963), and *Calamovilfa longifolia* var. *magna* (Thieret 1960) for confirmation.

Hagström (1916), when proposing that *P. richardsonii* arose as a hybrid between *P. praelongus* and *P. perfoliatus*, was correct in pointing out that *P. richardsonii* is intermediate in size and the fibrous nature of the stipules between the two putative parents. However, the stem anatomy being completely unlike *P. praelongus*, the flavonoid chemistry being non-additive, and the phylogeography all individually and collectively contradict Hagström's theory.

ACKNOWLEDGEMENTS

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REFERENCES

- ASCHERSON, P., and P. GRAEBNER. 1907. Potamogetonaceae. In: A. Engler. Das Pflanzenreich Regni Vegetabilis Conspectus 4(11):1-183. Wilhelm Engelmann, Leipzig.
- FERNALD, M. L. 1932. The linear-leaved North American species of *Potamogeton* section *Axillares*. Mem. Amer. Acad. Arts 17:1-183 (Also, Mem. Gray Herb. No. 3).

- GUIRE, K. E., and E. G. VOSS. 1963. Distributions of distinctive shoreline plants in the Great Lakes region. *Michigan Bot.* 2:99–114.
- HAGSTÖM, J.O. 1916. Critical researches on the Potamogetons. *Kongl. Svenska Vetenskapsakad. Handl.* 55(5):1–281.
- HARBOURNE, J. B., and C. A. WILLIAMS. 1976. Occurrence of sulphated flavones and caffeic acid esters in members of the Fluviales. *Biochem. Syst. & Ecol.* 4:37–41.
- HAYNES, R. R. 1974. A revision of North American *Potamogeton* subsection *Pusilli* (Potamogetonaceae). *Rhodora* 76:564–649.
- HAYNES, R. R. 1978. The Potamogetonaceae in the southeastern United States. *J. Arnold Arb.* 59:170–191.
- HAYNES, R. R., and D. C. WILLIAMS. 1975. Evidence for the hybrid origin of *Potamogeton longiligulatus* Fern (Potamogetonaceae) *Michigan Bot.* 14:94–100.
- HOLMGREN, P. K., et al. 1981. *Index Herbariorum*. Pt. 1. The Herbaria of the World. 7th ed. Dr. W. Junk B. V., Publ. The Hague. 452 pp.
- HULTEN, E. 1937. Outline of the history of arctic and boreal biota during the quaternary period. *Bokforlags Aktiebolaget Thule*, Stockholm. 168 pp + 43 pl.
- ILTIS, H. H. 1965. The genus *Gentianopsis* (Gentianaceae): transfers and phylogeographic comments. *Sida* 2:129–153.
- JOHNSON, M. E., and H. H. ILTIS. 1963. Preliminary reports on the flora of Wisconsin No. 48. Compositae I—Composite family 1. *Trans. Wisconsin Acad. Sci.* 52:255–342.
- JUZEPČZUK, S. V. 1934. Potamogetonaceae. In: V. L. Komarov, *Flora of the U.S.S.R.* 1:229–265.
- OGDEN, E. C. 1943. The broad-leaved species of *Potamogeton* of North America north of Mexico. *Rhodora* 45:57–105, 119–163, 171–214.
- ORNDUFE, R., et al. 1973. Flavonoids of artificial interspecific hybrids in *Lasthenia*. *Biochem. Syst.* 1:147–151.
- RAUNKIAER, C. 1896. *De Danske Blomsterplanter Naturhistorie I. Helobiacae*. Copenhagen.
- RAUNKIAER, C. 1903. Anatomical *Potamogeton*-studies and *Potamogeton fluitans*. *Bot. Tidsskr.* 25:253–380.
- ROBERTS, M. L., and R. R. HAYNES. (submitted) Leaf flavonoid chemistry of *Potamogeton* subsections *Praelougi* and *Perfoliati*. *Nordic J. Bot.*
- ROLÉ, E. J., et al. 1977. Numerical taxonomy system of Multivariate statistical programs. Program printout.
- THIERET, J. W. 1960. *Calamovilfa longifolia* and its variety *magna*. *Amer. Midl. Naturalist* 63:169–176.